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Soil aluminium effects on uptake, influx, and transport of nutrients in sorghum genotypes

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Abstract

Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth most important cereal crop of the world. In South America, it is grown mainly on acid soils, and its production on these soils is limited by deficient levels of available P, Ca, Mg, and micronutrients, and toxic levels of Al and Mn. A greenhouse experiment was undertaken to evaluate the genotypic differences in sorghum for uptake (U), inhibition (IH), influx (IN) into roots, and transport (TR) to shoot for nutrients at three levels of soil Al saturation (2, 41, 64%). Overall shoot nutrient U, IN, and TR showed a significant inverse correlation with soil Al saturation and shoot Al concentration, and a significant positive correlation with shoot and root dry weight. The nutrient uptake parameters differentiated genotypes into most and least efficient categories at various levels of soil Al saturation. The nutrient uptake parameters showed significant differences with respect to soil Al saturation, genotypes, and their interactions. In the current study, Al tolerant genotypes recorded higher IN and TR for P, K, Ca, Mg, Zn, and Fe than Al-sensitive genotypes. Therefore, these U, IN, and TR traits could be used in selection of sorghum plants adaptable to acid soils. Sorghum genotypes used in this study showed intraspecific genetic diversity in U, IN, and TR for essential nutrients. It was concluded that selection of acid soil tolerant genotypes and further breeding of acid (Al) tolerant sorghum cultivars are feasible.

Introduction

In Latin America, sorghum [*Sorghum bicolor* (L.) Moench] is grown on 4.6 million ha (Sere and Estrada, 1987). The majority of soils in this area are acidic, and crop production is limited by toxic levels of Al and Mn and low levels of P, Ca, Mg, and micronutrients (Sanchez and Salinas, 1981).

Chemical constraints for crop production on acid soils can be overcome by the addition of lime and fertilizers. For many farmers in this area, the use of chemical amendments is a costly input. The use of acid soil tolerant plants will help to reduce the cost of crop production in these areas. Genetic differences in nutrient concentrations, uptake, nutrient use efficiency, and transport have been reported for sorghum cultivars and genotypes subjected to aluminum stress (Baligar et al., 1989; Clark et al., 1988; Clark and Gourley, 1987, 1988; Duncan, 1983; Malavolta et al., 1981). Genotypes having high yield potentials and efficient nutrient use, both in the absence and presence of Al, will be useful to breeders in producing cultivars with high adaptability to acid soils.

The objective of our study was to evaluate the effects of soil Al levels on uptake, influx, and transport of essential nutrient elements in 40 sorghum genotypes. Growth differences in these sorghum genotypes due to soil aluminum have been reported earlier (Baligar et al., 1989).

Materials and methods

Forty sorghum genotypes and hybrids were selected for the study (Table 1). Details of the experimental methods and soil chemical characteristics are given in an earlier paper (Baligar et al., 1989). Dark red latosol (Typic haplorthox) under Cerrado vegetation was collected from the 15 cm surface soil layer, air-dried, and passed through a 2-mm sieve. The unamended soil had 64% Al saturation with a pH of 4.3 (1:1 soil:H_2O). Two additional soil Al saturations (41% and 2%) were achieved by the addition of lime (54% CaO, 20% MgO, 125% neutralization). All of the Al levels received 140, 150, and 190 kg ha^{-1} of N, P, and K, respectively, as NH_4NO_3 and KH_2PO_4. In addition, 10 kg Zn ha^{-1} was added as $ZnSO_4\ 7H_2O$. Experiments were carried out in a greenhouse during November and December. Details of growth containers and growing conditions are given in an earlier paper (Baligar et al., 1989). On the 28th day after seedling, plants were harvested, shoots and roots were separated and thoroughly washed in distilled water, dried for a week at 60°C, and weighed. Shoot samples were ground to pass a 0.5 mm stainless steel screen and digested in a HNO_3-H_2SO_4-$HClO_4$ (10:1:4) mixture. Digest were analyzed for N, P, K, Ca, Mg, Zn, Fe, and Al. Details of the analytical methods are given in our earlier paper (Baligar et al., 1989). Percent nutrient uptake inhibition (IH), ion influx (IN), and ion transport (TR) were calculated as follows (Baligar, 1987; Baligar et al., 1987):

$$\%\,IH = [(U_0 - U_1)/U_0] \times 100 \tag{1}$$

where U refers to elemental content (m moles/5 plant) in shoot. Subscript 0 represents 2% soil Al

Table 1. Sorghum genotypes and hybrids used in the study[a]

No.	Genotype	Origin	Tolerance[b]	No.	Genotype	Origin	Tolerance
1	IS7173C	Tanzania	T	21	IS5769C	India	MS
2	CMS XS 101B	Via USA	S	22	IS5892C	India	MS
3	IS1140C	India	S	23	IS6398C	India	S
4	IS1141C	India	MS	24	IS6456C	India	MS
5	IS1143C	India	S	25	IS2508C	Sudan	MS
6	IS1151C	India	MS	26	CMS XS 116R	Ethiopia	MT
7	IS1207C	Malawi	MS	27	IS1335C	India	T
8	IS1526C	India	S	28	IS12564C	Sudan	T
9	IS2169C	Nigeria	MS	29	CMS XS 903	Via USA	S
10	IS2177C	India	MS	30	CMS XS 112B	Via USA	MS
11	IS2477C	Ethiopia	S	31	CMS XI 110	Via USA	MS
12	IS2501C	Sudan	MS	32	BR006R	Ethiopia	T
13	IS2757C	Uganda	T	33	CMS XS 102B	Via USA	T
14	IS3071C	Sudan	T	34	BR003R	Via USA	MT
15	IS3911C	India	MT	35	BR004	Via USA	MS
16	IS3956C	Nepal	MS	36	CMS XS 604	Via USA	MT
17	IS4839C	India	S	37	CMS XS 315	Hybrid	T
18	IS5530C	India	MS	38	BR600	Hybrid	MT
19	IS5554C	India	S	39	BR300	Hybrid	T
20	IS5747C	India	MS	40	CMS XS 304	Hybrid	MS

[a]Compiled from Schuering and Miller, 1978.
[b]Based on performance at 41% soil Al saturation. Where T = tolerant TI ≥ 60; MT = moderately tolerance TI > 45 to <60; MS = moderately sensitive TI > 30 to <45; S = sensitive TI ≤ 30.

saturation, and subscript 1 refers to 41 or 64% soil Al saturation.

$$IN = [(U_2 - U_1)/(T_2 - T_1)][(\ln RW_2 - \ln RW_1)/(RW_2 - RW_1)] \quad (2)$$

where U refers to elemental content (m moles/5 plant) in shoot. RW refers to root weight (g/5 plant). T refers to time in seconds. Subscripts 1 and 2 refer to initial (9 days) and final (28 days) sampling time. IN is expressed as p moles g^{-1} root sec^{-1}.

$$TR = [(U_2 - U_1)/(T_2 - T_1)][(\ln SW_2 - \ln SW_1)/(SW_2 - SW_1)], \quad (3)$$

where SW refers to shoot weight (g/5 plant); others are similar to equation 2. TR is expressed as p moles g^{-1} shoot sec^{-1}. Tolerance index (TI) was calculated as follows:

$$TI = (\text{Growth with Al}/\text{Growth without Al}) \times 100 \quad (4)$$

where with Al refers to 41% soil Al saturation and without Al refers to 2% soil Al saturation.

Results and discussion

Elemental concentration differences in sorghum genotypes, either in the presence or absence of Al, have been reported (Clark et al., 1988; Clark and Gourley, 1987, 1988; Duncan et al., 1980, 1983; Duncan, 1981, 1983). However, information on U, IH, IN, and TR of essential nutrients in sorghum, either in the presence or absence of Al in the growth medium, is somewhat limited. The following discussion focuses on nutrients and Al uptake parameters of sorghum genotypes/line in response to soil Al saturation of 41% and 2%. At 64% soil Al saturation, shoot and root growth was reduced by >88% (Baligar et al., 1989) and did not allow further significant discrimination of genotypes.

Uptake and inhibition of nutrients

At 41% soil Al saturation, uptake of essential elements in sorghum genotypes was reduced by 5 to 77% as compared to uptake at 2% soil Al saturation (Table 2). When soil Al saturation was increased to 64%, the uptake of nutrients was inhibited to the extent of 74% to 97% of uptake at 2% Al saturation. Reduction of elemental uptake with increasing soil Al saturation is related to both reduced dry matter and elemental concentrations. It has been reported that in plants Al decreases Ca and Mg concentrations much more than K concentrations (Baligar and Smedley, 1989; Rengel and Robinson, 1989). Uptake of various elements showed a highly significant ($p <$

Table 2. Mean values for U, IH, IN, and TR for various elements at 2%, 41%, and 64% soil Al saturation

Element	Soil-Al saturation (%)	Parameters[a]			
		U	IH	IN	TR
N	2	5.81	–	–	–
	41	2.53	65	–	–
	64	0.50	94	–	–
P	2	0.13	–	276.0	99.2
	41	0.06	57	170.8	68.7
	64	0.01	93	44.0	17.5
K	2	2.24	–	5174.0	1872.6
	41	0.71	69	2402.3	982.6
	64	0.12	95	1041.1	439.4
Ca	2	0.39	–	926.0	337.0
	41	0.11	75	376.7	158.7
	64	0.01	97	111.1	47.3
Mg	2	0.34	–	788.0	284.8
	41	0.08	77	269.8	112.7
	64	0.01	97	60.5	25.1
Zn	2	1.94	–	4.5	1.7
	41	1.99	5	7.0	2.8
	64	0.48	74	4.6	2.0
Fe	2	11.33	–	25.3	9.3
	41	4.71	58	16.3	6.8
	64	0.98	91	7.7	3.3
Al	2	21.04	–	46.5	17.5
	41	12.02	39	40.7	17.0
	64	3.06	84	24.1	10.4

[a]U = m moles/5 plants, divided by 10^3 for Zn, Fe, Al.
IH = %
IN = p moles g^{-1} root sec^{-1}.
TR = p moles g^{-1} shoot sec^{-1}.

0.01) negative correlation with soil Al saturation and invariably a significant negative relationship to shoot Al concentrations (Table 3). In various plant species, Al is known to suppress the uptake of many essential nutrients (Clark, 1984; Fageria et al., 1990; Foy, 1984).

Highly positive significant ($p < 0.01$) correlations were observed between uptake of elements and shoot and root weight (Table 3). Plant nutrient requirement is driven mostly by rate of growth and internal ionic concentrations (Pitman, 1972; White, 1973). At 64% soil Al saturation, dry matter accumulation by all genotypes was reduced drastically, thereby reducing plant demand for nutrients. Al-tolerant genotypes grown at 41% Al saturation recorded higher elemental uptake than Al-sensitive genotypes (Table 4). This is a reflection of their ability to accumulate higher

Table 3. Correlation coefficient values (r) for U, IN, and TR of different elements against soil Al-saturation, shoot-Al concentration, and growth of shoots and roots

Variables	Al sat.	Shoot Al concen.	Shoot weight	Root weight
Uptake (U)				
N	−0.81**	−0.21**	0.97**	0.86**
P	−0.81**	−0.19*	0.97**	0.84**
K	−0.80**	−0.25*	0.97**	0.84**
Ca	−0.87**	−0.25*	0.96**	0.88**
Mg	−0.86**	−0.26**	0.97**	0.87**
Zn	−0.39**	−0.04NS	0.70**	0.55**
Fe	−0.83**	−0.08NS	0.96**	0.87**
Al	−0.71**	0.21**	0.83**	0.76**
Influx (IN)				
P	−0.67**	−0.11*	0.82**	0.59**
K	−0.73**	−0.22**	0.89**	0.66**
Ca	−0.83**	−0.22**	0.88**	0.70**
Mg	−0.84**	−0.23**	0.90**	0.72**
Zn	0.05NS	0.05NS	0.29**	0.06NS
Fe	−0.66**	0.08NS	0.80**	0.58**
Al	−0.34**	0.52**	0.48**	0.32**
Transport (TR)				
N	–	–	–	–
P	−0.71**	−0.03NS	0.77**	0.70**
K	−0.82**	−0.15*	0.86**	0.81**
Ca	−0.90**	−0.17**	0.83**	0.84**
Mg	−0.92**	−0.19**	0.87**	0.86**
Zn	0.14NS	0.16**	0.13*	0.03NS
Fe	−0.68**	0.26**	0.68**	0.68**
Al	−0.29**	0.72**	0.32**	0.32**

*, **Significant at 0.05 and 0.01 levels of probability, respectively. NS = Not significant.

Table 4. Average values for U, IH, IN, and TR of elements in Al-sensitive and Al-tolerant genotypes at 41% soil Al saturation

Element	Parameters[a]			
	U	IH	IN	TR
Al-sensitive[b]				
N	0.93	79	–	–
P	0.02	80	48.6	23.9
K	0.18	89	752.7	407.7
Ca	0.04	89	149.3	88.7
Mg	0.03	90	105.8	56.2
Zn	0.49	72	2.3	1.2
Fe	1.64	82	7.4	3.9
Al	3.98	73	16.6	8.7
Al-tolerant[c]				
N	4.02	47	–	–
P	0.09	23	278.5	91.6
K	1.24	32	3723.1	1340.9
Ca	0.30	48	504.5	180.9
Mg	0.13	55	372.0	133.7
Zn	3.67	−71	11.1	4.0
Fe	8.01	21	24.0	8.6
Al	20.10	−14	59.2	21.2

[a]Similar to Table 2.
[b]Al-sensitive where TI − Shoot ≤ 30 includes genotypes 2, 3, 5, 8, 10, 11, 17, 19, 23, and 29.
[c]Al-tolerant where TI − Shoot ≥ 60 includes genotypes 1, 13, 14, 27, 28, 32, 33, 37, and 39.

dry matter at 41% soil Al saturation. On an acid Ultisol of Colombia, Clark et al. (1988) reported that, at 40% soil Al saturation, tolerant sorghum genotypes gave higher dry matter yields and lower concentrations of N, P, and S than susceptible genotypes; and at 60% soil Al saturation, tolerant genotypes had higher dry matter yields and concentrations of Ca and S and lower concentrations of P, S, Al, and Fe than the susceptible genotypes.

Genotype CM XS 604 most efficient in uptake of N, P, K, Ca, and Mg at 2% soil Al saturation, and it was also most efficient in uptake of N, K, and Zn at 41% soil Al saturation (Table 5). Genotype IS2177C was inefficient in uptake of N, Ca, Mg, and Fe at 2% soil Al saturation. Sensitive genotypes IS1140C, IS1143C, and IS1526C were inefficient in uptake of P, Mg, Zn, and Fe at 41% soil Al saturation. These results clearly show the existence of genetic diversity in sorghum genotypes for uptake of various essential elements. Based on analysis of variance, uptake of essential nutrients and Al was affected signifi-

Table 5. The U, IN, and TR of most efficient (E) and most inefficient (I) sorghum genotypes at 2%, 41%, and 64% soil Al saturation[a]

Element	Soil-Al sat. %	Uptake E Genotype no	U	Uptake I Genotype no.	U	Influx E Genotype no.	IN	Influx I Genotype no.	IN	Transport E Genotype no.	TR	Transport I Genotype no.	TR
N	2	36	10.73	10	3.09	–	–	–	–	–	–	–	–
	41	36, 39	5.70	5	0.47	–	–	–	–	–	–	–	–
	64	36	1.05	8	0.20	–	–	–	–	–	–	–	–
P	2	25,36,39	0.21	20,23	0.06	9	511.9	23	87.8	30	148.3	23	46.7
	41	14	0.12	3,5,8	0.01	1	381.0	5	−18.9	1	150.5	5	−11.9
	64	36,37	0.02	16	0.01	27	244.7	16,18	−18.1	33	71.1		−10.6
K	2	36	4.47	5	1.15	9	9732.0	10	2846.0	29,33	2762.0	5	1155.0
	41	36	1.98	5	0.08	36	5540.7	5	323.0	36	1844.5	5	182.7
	64	36	0.26	17	0.04	27	3084.0	17	239.3	33	1080.0	7,17	115.5
Ca	2	36	0.69	10	0.20	36	1399.5	10	450.3	4	416.0	10	244.0
	41	39	0.36	3	0.02	32	982.1	3,23	111.0	34	341.6	10	68.9
	64	26	0.02	8	0.01	26,27	266.4	2,8	44.1	26,37	88.7	10	20.2
Mg	2	36	0.62	5,10	0.17	9	1256.3	10	378.5	29	360.7	5	166.6
	41	39	0.27	3,5	0.01	36,37	643.3	3,5,23	71.2	34,35, 37,39	231.0	5	35.2
	64	36	0.02	8	0.01	26,27	153.4	16	2.2	29	56.4	16	−0.4
Zn	2	38	3.27	20	0.88	30,33	7.9	8	1.4	29	3.4	8	0.6
	41	36	7.11	3,5,8	0.16	36,37	18.7	5,8	0.9	36	6.7	5	4.9
	64	38	1.33	8,16,17	0.16	30,38,40	9.8	5,8,17	1.7	30,38,40	3.6	16,17	0.8
Fe	2	25	17.97	10	5.51	9	44.1	10	11.1	29	20.6	10,12	5.9
	41	39	13.22	3,5,8	0.86	37	35.5	5,8	3.9	9,37	12.4	5,8	2.2
	64	38	2.65	8	0.38	38	17.3	11	2.2	1,25	7.9	10,11	1.0
Al	2	29	37.81	10	11.21	29	84.3	19	16.7	29	48.7	19	6.0
	41	39,37	39.42	5,8	2.93	9,37	122.5	5,8	7.3	9	50.9	8	3.9
	64	38	11.72	9	1.07	38	79.6	9,15	3.2	38	30.4	9,15	1.1

[a]U = m moles/5 plant divided by 10^3 for Zn, Fe, and Al; IN = p moles g^{-1} root sec^{-1}; TR = p moles g^{-1} shoot sec^{-1}.

cantly ($p < 0.01$) by soil Al saturation, genotypic differences, and Al saturation × genotypic interactions (Table 6). Uptake of elements responded linearly, based on fitted orthogonal polynomials.

Influx (IN) and transport (TR) of nutrients

The IN and TR for P, K, Ca, Mg, Fe, and Al were reduced by increasing soil Al saturation from 2% to 64% (Table 2). With the exception of Zn and Fe, significant inverse relationships were observed between IN and TR, and soil Al saturation and shoot Al concentration (Table 3). In four annual ryegrass cultivars, Rengel and Robinson (1989) have reported a decrease in the average net influx of Ca and Mg, when Al levels of the growth medium increased from 0 to 592 μmol L^{-1}. However, K influx in their study increased up to 74 μmol L^{-1} of Al, then declined as the Al level increased. In the current study, with the exception of Zn, IN and TR for various elements were significantly correlated to shoot and root dry matter accumulation (Table 3).

Reduction in shoot and root growth due to Al toxicity or direct Al inhibition of nutrient uptake appeared to be a major factor in reduction in rate of IN and TR for various elements (Fageria et al., 1988, 1990; Foy, 1984;). Root morphological parameters such as length, surface area, volume, dry weight (Balligar, 1985; Hackett, 1969; Russell

Table 6. Analysis of variance (F value) for treatment effects on elemental U, IN, and TR

Variables	Variable				
	Al-sat.	Genotype (g)	Al-sat. × g	Among Al-sat.	
				linear	nonlinear
Uptake					
N	895.8**	11.2**	3.0**	1791.3**	0.3NS
P	920.2**	10.9**	3.9**	1839.4**	1.1NS
K	1068.5**	12.9**	4.9**	2114.5**	22.6**
Ca	1411.1**	9.3**	3.5**	2772.6**	49.6**
Mg	1449.4**	9.8**	3.8**	2814.6**	84.2**
Zn	270.1**	19.2**	7.5**	313.4**	226.2**
Fe	1004.8**	9.8**	3.9**	2009.3**	0.3NS
Al	665.4**	11.6**	7.3**	1302.7**	28.2**
Influx					
P	396.4**	10.8**	3.4**	751.0**	32.5**
K	515.6**	10.4**	3.2**	997.4**	2.2NS
Ca	731.3**	5.7**	2.4**	1410.8**	4.9*
Mg	877.0**	6.7**	2.6**	1683.9**	16.2**
Zn	48.1**	13.2**	3.9**	4.0*	85.1**
Fe	281.6**	7.0**	2.7**	511.5**	9.9**
Al	84.4**	8.9**	5.9**	124.2**	29.2**
Transport					
P	1864.8**	46.7**	12.4**	330.9**	315.2**
K	5018.6**	80.5**	20.2**	9561.1**	1.0NS
Ca	8620.8**	53.4**	20.6**	16407.7**	0.3NS
Mg	9687.0**	52.2**	15.1**	18480.0**	37.9**
Zn	554.6**	102.4**	26.9**	177.4**	833.6**
Fe	1509.1**	40.2**	17.6**	2494.7**	173.4**
Al	343.8**	51.2**	35.4**	355.9**	246.3**

*, **Significant at 0.05 and 0.01 levels of probability, resp. NS = Not significant.

and Sanderson, 1967), and physiological conditions of plants (Drew et al., 1969; Pitman, 1972) are known to affect plant nutrient uptake, IN, and TR. Aluminum has been known to affect many of the root and shoot morphological and physiological parameters (Fageria et al., 1988; Foy, 1984). In our study, Al-tolerant genotypes overall recorded higher IN and TR for all the essential elements under consideration, and also had higher IN and TR for Al (Table 4).

Genotypic differences were observed in IN and TR for various elements (Table 5). The most efficient and least efficient genotypes for IN and TR differed depending upon the level of soil Al saturation. At an Al saturation of 41%, genotype CMSXS604 was most efficient in IN for K, Mg, and Zn, and TR for K and Zn. Genotype CMSXS315 was most efficient in IN for Mg, Zn, Fe, and Al. Both of these genotypes are moderately tolerant and tolerant types for soil Al. At 41% soil Al saturation, genotype IS 1143C was most inefficient in IN and TR for P, K, Mg, Zn, and Fe, and this genotype was also most inefficient in uptake of these elements (Table 5). This is Al-sensitive genotype, however, Al-tolerant genotypes have greater potential for producing higher dry matter yields, mainly because they have higher efficiency for nutrient uptake parameters in presence of Al. Soil Al saturation, genotypes, and their interactions all significantly ($p < 0.01$) affected the IN and TR of various elements (Table 6). IN and TR significantly responded linearly to soil Al saturation, based on fitted orthogonal polynomials.

Conclusions

From the obtained results, it appears that the magnitude of uptake, influx, and transport of essential nutrient elements in sorghum genotypes are influenced by the level of Al toxicity in the growth medium and the ability of genotypes to tolerate the Al toxicity. Sorghum genotypes used in this study showed interspecific genetic diversity in nutrient uptake parameters, and such variation could be exploited in breeding programs to develop acid soil tolerant cultivars.

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